Response of plant physiological parameters to soil water availability during prolonged drought is affected by soil texture

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Abstract: Soil water deficit is increasingly threatening the sustainable vegetation restoration and ecological construction on the Loess Plateau of China due to the climate warming and human activities. To determine the response thresholds of *Amygdalus pedunculata* (AP) and *Salix psammophila* (SP) to soil water availability under different textural soils, we measured the changes in net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), leaf water potential (ψ_w), water use efficiency (WUE) and daily transpiration rate (T_d) of the two plant species during soil water content (SWC) decreased from 100% field capacity (FC) to 20% FC in the sandy and loamy soils on the Loess Plateau in the growing season from June to August in 2018. Results showed that P_n, G_s, WUE and T_d of AP and SP remained relatively constant at the beginning of soil water deficit but decreased rapidly as plant available soil water content (PASWC) fell below the threshold values in both the sandy and loamy soils. The PASWC thresholds corresponding to P_n, G_s and C_i of AP in the loamy soil (0.61, 0.62 and 0.70, respectively) were lower than those in the sandy soil (0.70, 0.63 and 0.75, respectively), whereas the PASWC thresholds corresponding to P_n, G_s and C_i of SP in the loamy soil (0.63, 0.68 and 0.78, respectively) were higher than those in the sandy soil (0.58, 0.62 and 0.66, respectively). In addition, the PASWC thresholds in relation to T_d and WUE of AP (0.60 and 0.58, respectively) and SP (0.62 and 0.60, respectively) in the loamy soil were higher than the corresponding PASWC thresholds of AP (0.58 and 0.52, respectively) and SP (0.55 and 0.56, respectively) in the sandy soil. Furthermore, the PASWC thresholds for the instantaneous gas exchange parameters (e.g., P_n and G_s) at the transient scale were higher than the thresholds for the parameters (e.g., T_d) at the daily scale. Our study demonstrates that different plant species and/or different physiological parameters exhibit different thresholds of PASWC and that the thresholds are affected by soil texture. The result can provide guidance for the rational allocation and sustainable management of reforestation species under different soil conditions in the loess regions.

Keywords: plant available soil water content; drought stress; soil water deficit; sustainable vegetation restoration; sandy soil; loamy soil; Loess Plateau

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1 Introduction

Soil moisture is an important factor limiting the productivity of terrestrial ecosystems in arid and semi-arid regions in the world (Huxman et al., 2004; Viciedo et al., 2021). Due to the influence of natural climate change and anthropogenic activities, the frequency and intensity of drought stress in plant growth in arid and semi-arid regions will continue to increase (Dai, 2011). Severe drought stress will result in significant decrease in soil water availability and plant productivity (Breshears et al., 2005; Allen et al., 2010; Ullah et al., 2019). Therefore, the response of plant physiological parameters to drought stress has been extensively studied by ecologists during the past several years (Sinclair et al., 2005; Yan et al., 2017a; Zhang et al., 2020). Studies have demonstrated that drought stress would cause damage to plant growth by limiting CO_2 uptake and reducing photosynthetic activity (Osakabe et al., 2014). However, different types of plants and different physiological parameters of the same plant show different sensitivities to the increasing intensity of drought stress (Blackman et al., 2009; Yan et al., 2017b). For instance, Blackman et al. (2009) examined changes in leaf water potential (ψ_w), leaf hydraulic conductance and midday transpiration in four temperate woody species (*Atherosperma moschatum*, *Tasmannia lanceolata*, *Lomatia tinctoria* and *Hakea lissosperma*) under different drought conditions. They found that the four species exhibited larger variations in drought tolerance that was closely related to the leaf hydraulic vulnerability. The species-specific variations in hydraulic properties play important roles in the rates of plant recovery during re-wetting. Yan et al. (2017b) investigated the response of different physiological parameters to prolonged drought in commonly reforested plants on the Loess Plateau of China. They defined the plant available soil water content (PASWC) as the ratio of soil water content (SWC) to field capacity (FC) (i.e., PASWC=SWC/FC). Results showed that leaf water status, gas exchange and fluorescence parameters all remained unchanged when PASWC was higher than a threshold value but changed rapidly when PASWC was lower than the threshold. Furthermore, the threshold values of PASWC varied significantly among different physiological parameters. For example, Wu and Huang (2010) pointed out that there were significant differences in PASWC thresholds of various physiological parameters in maize and the PASWC thresholds were significantly affected by soil texture. Because PASWC is one of the principal factors limiting plant growth and development in terrestrial ecosystems, quantifying the PASWC thresholds in different types of plants and soils can provide guidance for the sustainable vegetation restoration. Despite extensive research on plant physiological responses to soil water stress (Gallé et al., 2007; Osakabe et al., 2014; Bresson et al., 2015; Zhang et al., 2020), only a few studies have examined the quantitative relationships between the plant physiological parameters and SWC due to the site-specific differences (Sadras and Milroy, 1996; Soltani et al., 2000; Yan et al., 2017b). This results in difficulty in selecting proper evaluation parameters for PASWC in different types of plants and soils. Therefore, further research is required to quantitatively model how physiological parameters respond to PASWC under different soil texture and vegetation types.

The Loess Plateau of China suffers from severe erosion and water shortage (Wen and Deng, 2020). Large-scale afforestation on the Loess Plateau since 1999 accelerated soil water depletion, leading to the widespread formation and distribution of dried soil layer (Jia et al., 2015; Wang et al., 2018) that limits the reliability of soil water supply and threatens the sustainable vegetation restoration (Huang and Shao, 2019). Previous studies have shown that soil water availability remains relatively unchanged when SWC is higher than a threshold value but declines rapidly when SWC drops below the threshold (Bielorai, 1973; Huang and Shao, 2019). When SWC is higher than the PASWC threshold, the physiological parameters of the plants remain relatively stable even though the SWC is decreasing. However, when SWC is lower than the PASWC threshold, the physiological parameters of the plants will either decrease rapidly (e.g., net photosynthetic rate (P_n) and daily transpiration rate (T_d)) or increase rapidly (e.g., intercellular CO_2 concentration (C_i) and (ψ_w)) with the decrease of SWC (Bielorai, 1973; Sadars and Milroy, 1996; Huang and Shao, 2019). Sadars and Milroy (1996) pointed out based on a literature review that the PASWC threshold varies with plant types, physiological parameters and soil texture, and that plants of the same species but different genotypes also exhibit different PASWC thresholds. The Loess Plateau area exhibits large

spatial variations in soil texture and extensive distribution of artificial vegetation (Huang and Shao, 2019). The investigation of the PASWC thresholds of typical plants grown in soils with different texture types and their differences can provide a scientific basis for formulating suitable measures for vegetation restoration on the Loess Plateau according to local conditions. However, previous studies mainly focused on the PASWC thresholds of single crop on the Loess Plateau or on the PASWC thresholds of woods and grasses grown in soils of the same texture. There are few studies on the PASWC thresholds of typical plants in soils with different texture types. Thus, there is an urgent need to investigate the response thresholds of physiological parameters to prolonged drought in different textural soils and vegetation types; the results of which could provide guidance for the rational allocation and sustainable management of reforestation species under different soil and water conditions on the Loess Plateau.

Amygdalus pedunculata (AP) and *Salix psammophila* (SP) are excellent wind-preventing and sand-fixing tree species that are widely distributed on the northern Loess Plateau (Pei et al., 2021). In recent years, to speed up desertification control, national and local governments have grown and promoted AP and SP in large areas on the northern Loess Plateau. However, drought and water shortage are the key factors that limit the large-scale vegetation restoration in this region. The determination of the PASWC thresholds of AP and SP in soils with different texture types is of great importance to the rational layout and sustainable vegetation restoration. This study is oriented to characterize the response thresholds of P_n, stomatal conductance (G_s), C_i, ψ_w, water use efficiency (WUE) and T_d to prolonged drought in AP and SP under the sandy and loamy soils in the Liudaogou watershed on the northern Loess Plateau. The aim of this study is to: (i) determine how the physiological parameters (P_n, G_s, C_i, ψ_w, WUE and T_d) respond to PASWC; (ii) establish quantitative relationships between the physiological parameters and PASWC by multiple regressions; and (iii) quantify the PASWC thresholds in the two species under different textural soils. The results of this study are beneficial to determine soil WUE and can provide references for the rational allocation of vegetation in different textural soils on the Loess Plateau.

2 Materials and methods

2.1 Study area

This study was carried out in the Shenmu Erosion and Environmental Research Station, which is located in the Liudaogou watershed (38°46′–38°51′N, 110°21′–110°23′E) on the northern Loess Plateau, China. This area is affected by water and wind erosion. It has an average altitude of approximately 1178 m, an annual mean air temperature of 8.4°C and a mean annual precipitation of 442 mm. The precipitation is concentrated in the period from July to September, with heavy precipitation contributing to 70%–80% of the annual total. The landform of the study area is sheet sand-covered loess hilly land with a large variation in soil particle compositions. Soil type can be divided into sandy soil, loamy sand soil, sandy loam soil, silty loam soil and clay loam soil. The main component of soil particles in the area is silt. The proportion of silty loam soil area is approximately 39.3% of the total area, the proportion of sandy loam soil area is approximately 27.8%, the loamy sand soil area is approximately 16.2%, the sandy soil area is approximately 11.9% and the clay loam soil area is 4.8% (Mao et al., 2018). Natural vegetation in the Liudaogou watershed had been seriously damaged. Since farmland has been converted back to forest land and grassland, vegetation covers have been gradually improved. Currently, the vegetation in this watershed is mainly composed of artificial forests with main species such as *Prunus sibirica*, SP, AP, *Caragana microphylla*, *Medicago sativa*, *Amorpha fruticose* and *Imperata cylindrica* (Pei et al., 2021).

2.2 Sampling and analysis

Undisturbed soil samples in the depth of 0–30 cm were collected every 10 cm by stainless steel cutting rings in May 2018; these soil samples were used for measuring the bulk density (BD), FC and saturated hydraulic conductivity (K_s). BD and FC were determined by the method of Grossman and Reinsch (2002). K_s was determined by the constant hydraulic head method of Jury

and Horton (2004) at 10°C. Disturbed soil samples in the depth of 0–30 cm were also collected every 10 cm; these samples were prepared for determining soil organic carbon (SOC), soil total phosphorus (STP), soil total nitrogen (STN) and particle size distribution (PSD). SOC, STP and STN were measured using the $K_2Cr_2O_7$ oxidation method (Nelson and Sommers, 1996), the ascorbic acid molybdenum blue method (Murphy and Riley, 1962) and the Kjeldahl method (Bremner and Tabatabai, 2008), respectively. The soil particle size was determined by the MS2000 laser particle size analyzer (Malvern Instrument, Malvern, England). We classified the clay (<0.002 mm), silt (0.002–0.020 mm) and sand (0.020–2.000 mm) fractions according to the international texture classification system (Jury and Horton, 2004). The basic soil properties of the studied soils are listed in Table 1.

Table 1 Physical-chemical properties of the sandy and loamy soils in the study area

Soil type	BD (g/cm^3)	K_s at 10°C (cm/h)	FC (g/kg)	Clay (%)	Silt (%)	Sand (%)	SOC (g/kg)	STN (g/kg)	STP (g/kg)
Sandy soil	1.64	13.42	146.70	5.95	31.28	62.77	2.49	1.34	1.68
Loamy soil	1.37	8.21	273.37	13.88	50.13	35.99	3.27	1.52	1.48

Note: BD, bulk density; K_s, saturated hydraulic conductivity; FC, field capacity; SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorus.

2.3 Experimental design and measurement

Three-year-old seedlings of AP and SP grown in the Liudaogou watershed were selected as the experimental materials. The typical sandy and loamy soils in the watershed were collected and sieved using a 2-mm sieve after air-dried. Equal weights of loamy and sandy soils (20 kg) were separately put inside metal planters (height: 50 cm; diameter: 25 cm), added with water until saturation and kept still for 1–2 d. Then, seedlings of AP and SP were transplanted into these planters and managed regularly to keep the soils well-watered (80% FC). After one month, seedlings of AP and SP with similar heights (40–50 cm) and stem diameters (3–5 mm) were selected as test plants, with three plants in each pot. The plants were then supplied with sufficient water within one month before the start of the experiment (SWC was controlled at 80%–100% FC) to ensure the survival of all plants. The pots were randomly placed. All experiments were carried out under a movable outdoor rain shelter. Four combinations (sandy soil-AP, loamy soil-AP, sandy soil-SP and loamy soil-SP) were used in the experiment, with five replications for each combination. Soil surface was uniformly covered with gravels (the diameter of the gravel: 0.5–1.5 cm; thickness of each gravel layer: 2.0 cm) to inhibit evaporation of soil moisture. After the start of the experiment, the water supply was stopped for all plants, and the soil moisture was allowed to evaporate freely. The pots were weighted every two days until the SWC dropped from 100% FC (i.e., the corresponding FC of loamy soil: 273.4 g/kg; the corresponding FC of sandy soil: 146.7 g/kg) to 90% FC, 80% FC, 60% FC, 40% FC and 20% FC (the corresponding water contents in loamy soil were 246.0, 218.7, 164.0, 109.4 and 54.7 g/kg, respectively; the corresponding water contents in sandy soil were 132.1, 117.4, 88.0, 58.7 and 29.4 g/kg, respectively) in the growing season from June to August in 2018.

When SWC was maintained at a certain level (i.e., 100% FC, 90% FC, 80% FC, 60% FC, 40% FC and 20% FC) for 3–5 d by weighing and adding water into the soils, the physiological parameters (P_n, G_s, C_i, ψ_w, WUE and T_d) of seedlings of AP and SP were observed once every hour from 08:00 to 18:00 (LST). During the measurement period, some water was weighted and added into each pot to ensure that SWC was stable in each stage so that each plant was fully adapted to a certain SWC before the measurement of physiological parameters. The physiological parameters were measured using the photosynthetic apparatus. Specifically, a handheld photosynthesis system (LI-6400, LI-COR Inc., Nebraska, USA) was used to measure P_n, G_s, C_i, WUE and T_d. The ψ_w was measured by a water potential instrument Model PSYPRO (Wescor Corp., Logan, UT, USA) under each SWC treatment. Discs with the diameter of 6 mm were cut from the leaves of three plants and sealed in the C-52 sample chamber. Samples were equilibrated

for 30 min before the readings were recorded by a Wescor HR-33T microvoltmeter (Wescor Corp., Utah, USA) in the psychrometric mode.

2.4 Data analysis

The potted plants were weighed every two days using a high-sensitivity electronic scale (precision: 1 g), and the weights were recorded. The reduction in SWC was calculated using the difference between the weight in each measurement and the initial weight. We calculated the cumulative daily transpiration rate (T_c) of each treatment based on water balance. Most past studies used piecewise linear functions and nonlinear continuous functions to describe the relationship between the plant physiological parameters and SWC (Ray and Sinclair, 1997; Soltani et al., 2000; Lagergren and Lindroth, 2002). This study adopted the nonlinear continuous functions to fit the dynamic variation curves of soil water availability. The inflection point of each curve is the PASWC threshold of each parameter. The parameters related to the pot experiment was normalized using the standard parametric equation proposed by Ray and Sinclair (1997), i.e., the ratio of the average of observed values for different SWC treatments to the average of observed values for the treatment with the highest SWC (i.e., 100% FC). In this study, we calculated the PASWC as the ratio of SWC to FC (PASWC=SWC/FC) according to the method of Yan et al. (2017b).

The data analyses were performed by Statistical Product and Service Solutions (SPSS 24.0); the figures were plotted by the package Origin Pro 9.0.

3 Results

3.1 Relationships between the physiological parameters and PASWC

Table 2 shows the quantitative relationships between the physiological parameters (P_n, G_s, C_i, WUE and T_d) and PASWC for the two species (AP and SP) in different textural soils (i.e., loamy and sandy soil). Seedlings of AP and SP grown in soils with different texture types exhibited differences in the PASWC thresholds of different physiological parameters (Table 2). The nonlinear continuous functions could simulate the dynamic variation characteristics of physiological parameters of plants under different levels of PASWC, with R^2 ranging from 0.89 to 0.99 (P<0.001; Table 2).

3.2 Responses of the gas exchange parameters to drought stress in different textural soils

Figure 1 shows the dynamic variation characteristics of P_n, G_s and C_i of AP and SP in the loamy and sandy soils. With the decrease of PASWC, the P_n and G_s of AP and SP with different soil texture types exhibited the same trend, i.e., they remained approximately constant when the PASWC was above a certain threshold and dropped rapidly with the reduction of PASWC when the PASWC was below this threshold. However, AP and SP grown in soils with different texture types had different decrease rates of P_n and G_s and different PASWC thresholds (Table 2; Fig. 1). The PASWC thresholds in relation to P_n and G_s of AP in the loamy soil was 0.61 and 0.62, respectively, which were lower than the corresponding PASWC thresholds in the sandy soil (0.70 and 0.63, respectively) (Table 2). In contrast, the PASWC thresholds in relation to P_n and G_s of SP in the loamy soil (0.63 and 0.68, respectively) were higher than the corresponding PASWC thresholds in the sandy soil (0.58 and 0.62, respectively) (Table 2). The C_i of AP and SP grown in soils with different texture types increased with the decrease of PASWC, and the trend of C_i was opposite to those of P_n and G_s (Fig. 1). The PASWC threshold in relation to C_i of AP in the loamy soil (0.70) was lower than the corresponding PASWC threshold in the sandy soil (0.75) (Table 2). However, the PASWC threshold in relation to C_i of SP in the loamy soil (0.78) was higher than the corresponding PASWC threshold in the sandy soil (0.66) (Table 2).

3.3 Responses of the WUE and ψ_w to drought stress in different textural soils

Figure 2 shows the dynamic changes in the WUE and ψ_w with drought stress for AP and SP grown in the loamy soil and in the sandy soil. The WUE of AP and SP grown in soils with different texture

Table 2 Regression analysis for the variations of different physiological parameters (P_n, G_s, C_i, T_d and WUE) with PASWC of *Amygdalus pedunculata* (AP) and *Salix psammophila* (SP) in the sandy and loamy soils

Physiological parameter	Plant species	Soil type	Equation of regression	PASWC threshold	R^2
P_n	AP	Sandy soil	P_n=0.98(1+e$^{-6.16(\text{PASWC}-0.27)}$)	0.70	0.96
		Loamy soil	P_n=1.03(1+e$^{-8.56(\text{PASWC}-0.25)}$)	0.61	0.94
	SP	Sandy soil	P_n=1.03(1+e$^{-5.18(\text{PASWC}-0.21)}$)	0.58	0.90
		Loamy soil	P_n=1.20(1+e$^{-3.79(\text{PASWC}-0.41)}$)	0.63	0.89
G_s	AP	Sandy soil	G_s=1.05(1+e$^{-10.14(\text{PASWC}-0.27)}$)	0.63	0.96
		Loamy soil	G_s=1.07(1+e$^{-5.16(\text{PASWC}-0.30)}$)	0.62	0.96
	SP	Sandy soil	G_s=0.99(1+e$^{-7.14(\text{PASWC}-0.21)}$)	0.62	0.92
		Loamy soil	G_s=1.10(1+e$^{-5.29(\text{PASWC}-0.32)}$)	0.68	0.93
C_i	AP	Sandy soil	C_i=0.62e$^{-\text{PASWC}/0.41}$+0.95	0.75	0.93
		Loamy soil	C_i=0.37e$^{-\text{PASWC}/0.43}$+0.96	0.70	0.95
	SP	Sandy soil	C_i=1.09e$^{-\text{PASWC}/0.18}$+1.02	0.66	0.91
		Loamy soil	C_i=0.48e$^{-\text{PASWC}/0.28}$+0.99	0.78	0.89
T_d	AP	Sandy soil	T_d=1.06(1+e$^{-5.54(\text{PASWC}-0.28)}$)	0.58	0.91
		Loamy soil	T_d=1.07(1+e$^{-6.90(\text{PASWC}-0.19)}$)	0.60	0.90
	SP	Sandy soil	T_d=1.18(1+e$^{-3.66(\text{PASWC}-0.38)}$)	0.55	0.89
		Loamy soil	T_d=1.05(1+e$^{-7.27(\text{PASWC}-0.27)}$)	0.62	0.97
WUE	AP	Sandy soil	WUE=1.04(1+e$^{-6.92(\text{PASWC}-0.28)}$)	0.52	0.97
		Loamy soil	WUE=1.07(1+e$^{-10.27(\text{PASWC}-0.19)}$)	0.58	0.99
	SP	Sandy soil	WUE=1.02(1+e$^{-6.36(\text{PASWC}-0.16)}$)	0.56	0.95
		Loamy soil	WUE=1.05(1+e$^{-6.17(\text{PASWC}-0.25)}$)	0.60	0.98

Note: P_n, net photosynthetic rate; G_s, stomatal conductance; C_i, intercellular CO_2 concentration; T_d, daily transpiration rate; WUE, water use efficient; PASWC, plant available soil water content; R^2, coefficient of determination.

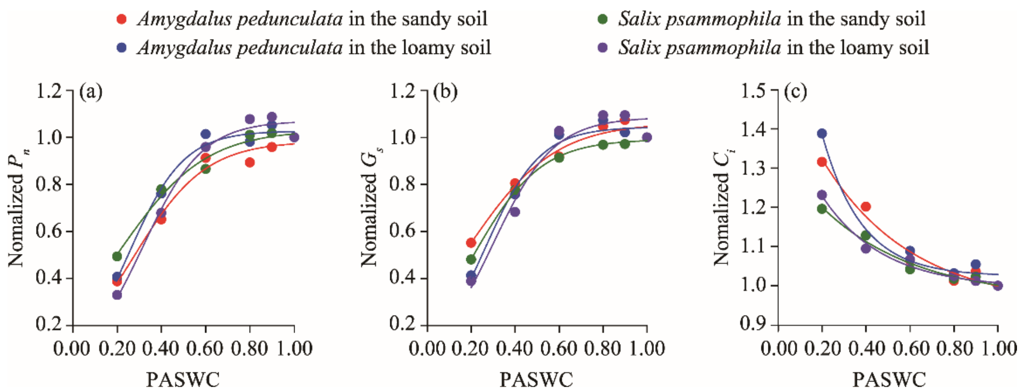

Fig. 1 Variations of normalized photosynthesis parameters P_n (a), G_s (b) and C_i (c) with PASWC of *Amygdalus pedunculata* (AP) and *Salix psammophila* (SP) in the sandy and loamy soils. P_n, net photosynthetic rate; G_s, stomatal conductance; C_i, intercellular CO_2 concentration; PASWC, plant available soil water content.

types remained relatively stable when PASWC was above a certain threshold and decreased rapidly with the reduction of PASWC when PASWC was below this threshold. The PASWC thresholds in relation to WUE of AP and SP in the loamy soil (0.58 and 0.60, respectively) were higher than the corresponding PASWC thresholds in the sandy soil (0.52 and 0.56, respectively) (Table 2). The ψ_w of AP and SP grown in soils with different texture types decreased linearly with the increase of PASWC (Fig. 2).

3.4 Responses of plant transpiration to drought stress in different textural soils

Figure 3 shows the dynamic variation characteristics of T_d and T_c of AP and SP under drought stress in the loamy soil and in the sandy soil. The T_d of AP and SP in soils with different texture types

remained relatively stable when PASWC was above the threshold value and decreased rapidly with the reduction of PASWC when PASWC was below this threshold. The PASWC thresholds in relation to T_d of AP and SP in the loamy soils (0.60 and 0.62, respectively) were higher than the corresponding PASWC thresholds in the sandy soil (0.58 and 0.55, respectively) (Table 2). In addition, the PASWC thresholds in relation to T_c of AP and SP in the loamy and sandy soils (0.42–0.48) were lower than the corresponding PASWC thresholds in relation to T_d (0.55–0.62) (Fig. 3).

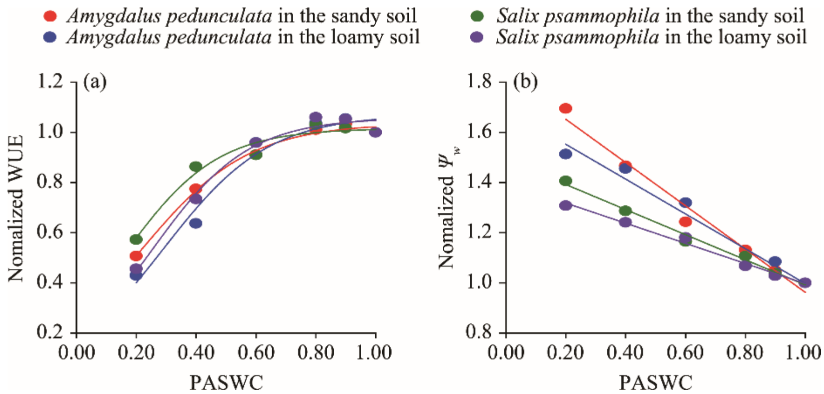

Fig. 2 Variations of normalized WUE (a) and Ψ_w (b) with PASWC of AP and SP in the sandy and loamy soils. WUE, water use efficiency; Ψ_w, leaf water potential.

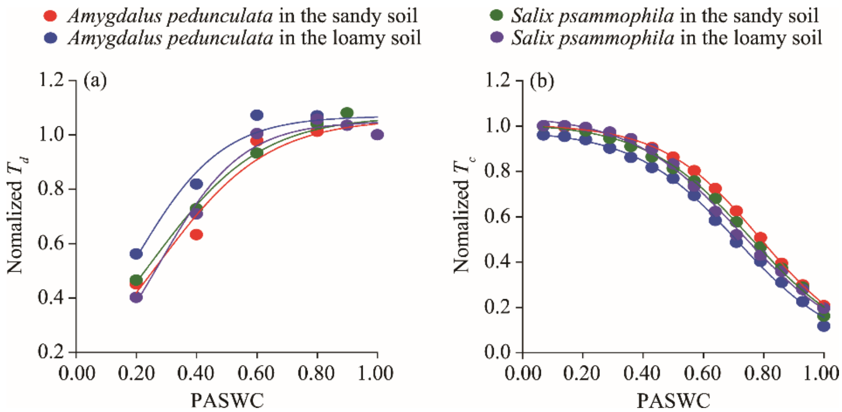

Fig. 3 Variations of normalized T_d (a) and T_c (b) with PASWC of AP and SP in the sandy and loamy soils. T_d, daily transpiration rate; T_c, cumulative daily transpiration rate.

4 Discussion

In arid and semi-arid regions, soil moisture is a key factor that limits plant growth and ecosystem evolution. Even in humid and semi-humid regions, plant species are commonly experiencing drought stress in the dry season (Marengo and Espinoza, 2016). During the growing season, plant roots absorb and consume large amounts of soil water, but the rates and mechanisms of soil water consumption differ markedly among different species. In addition, different plant species and/or different physiological parameters show different PASWC thresholds due to differences in phenological timing and changes in environmental conditions. As a consequence, a more accurate evaluation of the PASWC thresholds for different plant species grown in varying soil conditions is urgently needed (Sadras and Milroy, 1996; Soltani et al., 2000; Yan et al., 2017b). Previous studies showed that both leaf water status and gas exchanges can be used as indicators in the identification of drought, although the thresholds differ due to the different species, experimental conditions and evaluation methods (Soltani et al., 2000; Sinclair et al., 2005; Casadebaig et al., 2008; Wu and Huang, 2010; Pei et al., 2020). However, our results indicated that ψ_w is not a suitable indicator to

reflect the PASWC threshold. One possible reason is that PASWC used in this study did not decline low enough to cause the threshold changes in the ψ_w due to the relative high tolerance of drought stress of AP and SP. Moreover, the leaves of both AP and SP are very small that may affect the ability of ψ_w to show threshold changes. Thus, further verification of the experimental data in other plants with larger leaves is required.

A study of PASWC for different plant species on the Loess Plateau is necessary and important to the sustainable vegetation restoration due to the limited soil water resources. However, *in situ* investigation of the physiological responses to natural soil drought in the field is difficult, due to the spatial heterogeneity of soil texture, climatic conditions and vegetation types on the Loess Plateau (Huang and Shao, 2019). In the present study, pot experiments were conducted to provide information on the dynamic changes of the physiological parameters of AP and SP grown in different textural soils during prolonged drought and on their PASWC thresholds. The experimental results showed that the different physiological parameters (P_n, G_s, WUE and T_d) of AP and SP remained relatively constant at the beginning of soil water deficit but declined rapidly when PASWC fell below the threshold values in both loamy and sandy soils (Figs. 1–3). The quantitative relationships between the physiological parameters (P_n, G_s, WUE and T_d) and PASWC can be modelled by the nonlinear equations, with R^2 ranging from 0.89 to 0.99 (P<0.001; Table 2). Significant correlations between the physiological parameters (e.g., gas exchange parameters and leaf water status) and PASWC were also reported in other studies (Guo and Li, 1994; Casadebaig et al., 2008; Belko et al., 2012; Yan et al., 2017b). The PASWC thresholds for different physiological parameters of AP and SP varied due to the differences in phenological timing and changes in soil characteristics. For instance, the PASWC thresholds for the instantaneous gas exchange parameters (e.g., P_n and G_s) at the transient scale were higher than the thresholds at the daily scale (e.g., T_d) (Table 2), indicating that gas exchange parameters are more sensitive to soil water deficit (Medrano et al., 2002). The gas exchange responses to soil water stress thus were often used for determining the degree of drought conditions. The PASWC thresholds of P_n, G_s, C_i and T_d of AP (0.70, 0.63, 0.75 and 0.58, respectively) were higher than those of SP (0.58, 0.62, 0.66 and 0.55, respectively) in the sandy soil. In contrast, the PASWC thresholds of P_n, G_s, C_i and T_d of AP (0.61, 0.62, 0.70 and 0.60, respectively) were lower than those of SP (0.63, 0.68, 0.78 and 0.62, respectively) in the loamy soil. The results indicated that the PASWC thresholds are different between the studied species either in the sandy soil or in the loamy soil. This may be attributed to the different root structures and distributions of AP and SP, which requires further study. Many previous studies have demonstrated different response thresholds of gas exchange parameters in different plant species (Sinclair et al., 2005; Casadebaig et al., 2008) or under different experimental conditions (Sadras and Milroy, 1996; Soltani et al., 2000). It is well established that the stomatal closure drives the decline of plant transpiration and photosynthesis under mild to moderate drought conditions (Medrano et al., 2002; Yan et al., 2017b).

Our study also demonstrated that the PASWC thresholds of AP and SP are affected by soil texture (Table 2). The PASWC thresholds corresponding to P_n, G_s and C_i of AP in the loamy soil (0.61, 0.62 and 0.70, respectively) were lower than those in the sandy soil (0.70, 0.63 and 0.75, respectively), whereas the PASWC thresholds corresponding to P_n, G_s and C_i of SP in the loamy soil (0.63, 0.68 and 0.78, respectively) were higher than those in the sandy soil (0.58, 0.62 and 0.66, respectively). In addition, the PASWC thresholds in relation to T_d and WUE of AP (0.60 and 0.58, respectively) and SP (0.62 and 0.60, respectively) in the loamy soil were higher than the corresponding PASWC thresholds of AP (0.58 and 0.52, respectively) and SP (0.55 and 0.56, respectively) in the sandy soil. The differences in the PASWC thresholds in the sandy and loamy soils could be attributed to the differences in soil hydraulic properties (Fig. 4). The sandy soil has much higher hydraulic conductivity than the loamy soil (Table 1). Saliendra and Meinzer (1989) have shown that the decline in the hydraulic conductivity of the soils could cause reductions in G_s. Su et al. (2015) found that soil texture controls the growth and biomass of vegetation in arid desert grassland in the middle of Hexi Corridor region in Northwest China. Thus, soil texture is a key factor that controls plant response to soil water deficit. Considering the variations in the physiological parameters and PASWC thresholds of AP and SP in the loamy and sandy soils with

prolonged drought, we recommend to plant AP in the sandy soil and SP in the loamy soil on the Loess Plateau.

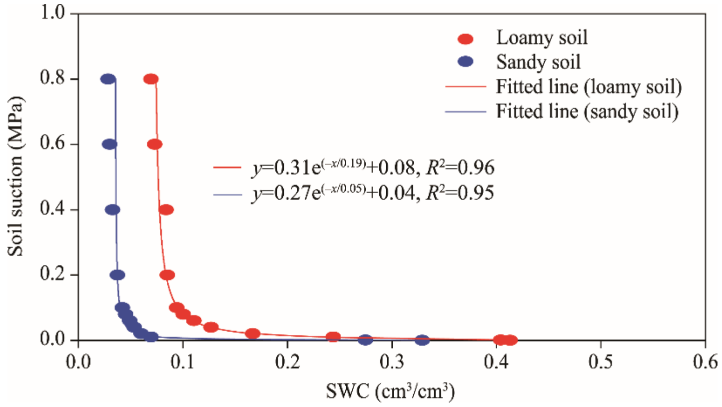

Fig. 4 Relationship between soil suction and SWC in the sandy and loamy soils. SWC, soil water content.

5 Conclusions

A pot experiment was designed and used to investigate the physiological responses of AP and SP to prolonged drought in two different textural soils on the Loess Plateau. Results showed that P_n, G_s, WUE and T_d of AP and SP remained relatively constant at the beginning of soil water deficit but decreased rapidly as PASWC fell below the threshold values in both the sandy and loamy soils. However, different plant species and/or different physiological parameters exhibited different thresholds of PASWC and the thresholds were affected by soil texture. Considering the variations in the physiological parameters and PASWC thresholds of AP and SP in the loamy and sandy soils with prolonged drought, we recommend to plant AP in the sandy soil and SP in the loamy soil on the Loess Plateau.

One limitation of this study is that the pot used for experiment may inhibit plant growth because of the limited space. As such, the extrapolation of the experimental data to the natural field requires further study. This study also suggests several future research directions. Firstly, we suggest a longitudinal and latitudinal design to examine the relationship and mechanisms between the plant physiological parameters and soil water conditions at larger spatial scales. Secondly, given that plant seedlings may respond differently to water stress compared with plants at later growth stages, for future research the inclusion of plants with different ages would help us to better understand the dynamics of the PASWC thresholds with different stages of plant growth. Finally, the development of quantitative models for predicting changes in the PASWC thresholds for typical arbor trees, shrubberies and grasses would also be interesting and meaningful.

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References

Allen C D, Macalady A K, Chenchouni H, et al. 2010. A global overview of drought and heat-induced tree mortality reveals

emerging climate change risks for forests. Forest Ecology and Management, 259(4): 660–684.

Belko N, Zaman-Allah M, Cisse N, et al. 2012. Lower soil moisture threshold for transpiration decline under water deficit correlates with lower canopy conductance and higher transpiration efficiency in drought-tolerant cowpea. Functional Plant Biology, 39(4): 306–322.

Bielorai H. 1973. Prediction of irrigation needs. In: Yaron B, Danfors E, Vaadia Y. Arid Zone Irrigation. Berlin: Springer, 359–369.

Blackman C J, Brodribb T J, Jordan G J. 2009. Leaf hydraulics and drought stress: response, recovery and survivorship in four woody temperate plant species. Plant, Cell & Environment, 32(11): 1584–1595.

Bremner J M, Tabatabai M A. 2008. Use of an ammonia electrode for determination of ammonium in Kjeldahl analysis of soils. Communications in Soil Science and Plant Analysis, 3(2): 159–165.

Breshears D D, Cobb N S, Rich P M, et al. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences of the United States of America, 102(42): 15144–15148.

Bresson J, Vasseur F, Dauzat M, et al. 2015. Quantifying spatial heterogeneity of chlorophyll fluorescence during plant growth and in response to water stress. Plant Methods, 11: 23, doi: 10.1186/s13007-015-0067-5.

Casadebaig P, Debaeke P, Lecoeur J. 2008. Thresholds for leaf expansion and transpiration response to soil water deficit in a range of sunflower genotypes. European Journal of Agronomy, 28(4): 646–654.

Dai A. 2011. Drought under global warming: A review. WIREs Climate Change, 2(1): 45–46.

Gallé A, Haldimann P, Feller U. 2007. Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery. New Phytologist, 174(4): 799–810.

Grossman R B, Reinsch T G. 2002. Bulk density and linear extensibility. In: Dane J H, Clarke Topp G. Methods of Soil Analysis: Part 4 Physical Methods. Madison: Soil Science Society of America, 201–228.

Guo Q R, Li Y S. 1994. Soil moisture availability to plant in the southern the Loess Plateau. Acta Pedologica Sinica, 31(3): 236–243. (in Chinese)

Huang L M, Shao M A. 2019. Advances and perspectives on soil water research in China's Loess Plateau. Earth-Science Reviews, 199: 102962, doi: 10.1016/j.earscirev.2019.102962.

Huxman T E, Smith M D, Fay P A, et al. 2004. Convergence across biomes to a common rain-use efficiency. Nature, 429(6992): 651–654.

Jia X X, Shao M A, Zhang C C, et al. 2015. Regional temporal persistence of dried soil layer along south–north transect of the Loess Plateau, China. Journal of Hydrology, 528: 152–160.

Jury W A, Horton R. 2004. Soil Physics (6^{th} ed.). New Jersey: John Wiley & Sons, Inc., 78–83.

Lagergren F, Lindroth A. 2002. Transpiration response to soil moisture in pine and spruce trees in Sweden. Agricultural and Forest Meteorology, 112(2): 67–85.

Mao N, Huang L M, Shao M A. 2018. Vertical distribution of soil organic and inorganic carbon under different vegetation covers in two toposequences of Liudaogou watershed on the Loess Plateau, China. Journal of Soil and Water Conservation, 73(4): 479–491.

Marengo J A, Espinoza J C. 2016. Extreme seasonal droughts and floods in Amazonia: causes, trends and impacts. International Journal of Climatology, 36(3): 1033–1050.

Medrano H, Escalona J M, Bota J, et al. 2002. Regulation of photosynthesis of C_3 plants in response to progressive drought: stomatal conductance as a reference parameter. Annals of Botany, 89: 895–905.

Murphy J, Riley J P. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta, 27: 31–36.

Nelson D W, Sommers L E. 1996. Total carbon, organic carbon, and organic matter. In: Sparks D L, Page A L, Helmke P A, et al. Methods of Soil Analysis Part 3: Chemical Methods. Madison: Soil Science Society of America, 961–1010.

Osakabe Y, Osakabe K, Shinozaki K, et al. 2014. Response of plants to water stress. Frontiers of Plant Science, 5: 86, doi: 10.3389/fpls.2014.00086.

Pei Y W, Huang L M, Shao M A, et al. 2020. Responses of *Amygdalus pedunculata* Pall. in sandy and loamy soils to water stress. Journal of Arid Land, 12(5): 791–805.

Pei Y W, Huang L M, Li D F, et al. 2021. Characteristics and controls of solute transport under different conditions of soil texture and vegetation type in the water-wind erosion crisscross region of China's Loess Plateau. Chemosphere, 273: 129651, doi: 10.1016/j.chemosphere.2021.129651.

Ray J D, Sinclair T R. 1997. Stomatal closure of maize hybrids in response to drying soil. Crop Science, 37(3): 803–807.

Sadras V O, Milroy S P. 1996. Soil-water thresholds for the responses of leaf expansion and gas exchange: a review. Field Crops Research, 47(2–3): 253–266.

Saliendra N Z, Meinzer F C. 1989. Relationship between root/soil hydraulic properties and stomatal behaviour in sugarcane. Australian Journal of Plant Physiology, 16(3): 241–250.

Sinclair T R, Holbrook N M, Zwieniecki M A. 2005. Daily transpiration rates of woody species on drying soil. Tree Physiology, 25(11): 1469–1472.

Soltani A, Khooie F R, Ghassemi-Golezani K, et al. 2000. Thresholds for chickpea leaf expansion and transpiration response to soil water deficit. Field Crops Research, 68(3): 205–210.

Su Y Z, Wang J Q, Yang R, et al. 2015. Soil texture controls vegetation biomass and organic carbon storage in arid desert grassland in the middle of Hexi Corridor region in northwest China. Soil Research, 53(4): 366–376.

Ullah H, Santiago-Arenas R, Ferdous Z, et al. 2019. Improving water use efficiency, nitrogen use efficiency, and radiation use efficiency in field crops under drought stress: a review. Advances in Agronomy, 156: 109–157.

Viciedo D O, Prado R D M, Martinez C A, et al. 2021. Changes in soil water availability and air-temperature impact biomass allocation and C:N:P stoichiometry in different organs of *Stylosanthes capitata* Vogel. Journal of Environmental Management, 278: 111540, doi: 10.1016/j.jenvman.2020.111540.

Wang Y Q, Shao M A, Zhu Y J, et al. 2018. A new index to quantify dried soil layers in water-limited ecosystems: a case study on the Chinese Loess Plateau. Geoderma, 322: 1–11.

Wen X, Deng X Z. 2020. Current soil erosion assessment in the Loess Plateau of China: a mini-review. Journal of Cleaner Production, 276: 123091, doi: 10.1016/j.jclepro.2020.123091.

Wu Y Z, Huang M B. 2010. Effect of soil texture on soil water availability for different maize physiological indices. Transactions of the Chinese Society of Agricultural Engineering, 26(2): 82–88. (in Chinese)

Yan W M, Zhong Y Q W, Shangguan Z P. 2016. A meta-analysis of leaf gas exchange and water status responses to drought. Scientific Reports, 6: 20917, doi: 10.1038/srep20917.

Yan W M, Zhong Y Q W, Shangguan Z P. 2017a. Rapid response of the carbon balance strategy in *Robinia pseudoacacia*, and *Amorpha fruticosa* to recurrent drought. Environmental and Experimental Botany, 138: 46–56.

Yan W M, Zhong Y Q W, Shangguan Z P. 2017b. Responses of different physiological parameter thresholds to soil water availability in four plant species during prolonged drought. Agricultural and Forest Meteorology, 247: 311–319.

Zhang Z D, Huang M B, Yang Y N, et al. 2020. Evaluating drought-induced mortality risk for *Robinia pseudoacacia* plantations along the precipitation gradient on the Chinese Loess Plateau. Agricultural and Forest Meteorology, 284: 107897, doi: 10.1016/j.agrformet.2019.107897.